

variation in electron microscope images resulting from different fixations. A prominent part of the plastid, a ringlike, apparently proteinaceous inclusion, is preserved by osmic acid but is eliminated in fixations with potassium permanganate. The external sculpturing of the plastid likewise is not preserved by potassium permanganate.

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CARBON ASSIMILATION OF MARINE PHYTOPLANKTON IN ANTARCTICA*

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Photosynthesis in natural populations of marine phytoplankton is of great interest to algal physiologists and to those who are concerned with estimates of primary organic production in the ocean. Although extensive studies have been devoted to the floristic features of the phytoplankton in south polar seas,¹⁻⁴ only recently have the seas of Antarctica, with their special properties of daylight, low temperature, high content of inorganic macronutrients, and interesting blooms of microalgae, become attractive to students of phytoplankton physiology. Since 1960, several investigators have initiated studies of primary production in Antarctica, with the carbon-14 method. In making calculations of productivity in Antarctic waters, Saijo and Kawashima⁵ estimated the assimilation number of the phytoplankton to be about 1.22 during the summer. The investigations of El Sayed *et al.*,⁶ in the Drake Passage and Bransfield Strait, revealed photosynthetic indices varying over the wide range of 2.61–10.47 for late summer populations, based upon light incubation of plankton at about 2500 foot candles (ft-c). The studies of Bunt^{7, 8} and Burkholder and Mandelli⁹ on microalgae in sea ice have demonstrated interesting properties of ice-adapted communities of diatoms.

In view of the need to know more about the assimilation coefficient and the relation of carbon fixation in Antarctic phytoplankton to the intensity of light, investigations were carried out on the Argentine icebreaker *General San Martin* during the period of February–March 1965, in the general region along the west coast of the Antarctic Peninsula, including the Bransfield Strait, Gerlache Strait, and the Bellingshausen Sea.

Materials and Methods.—Samples of sea water were obtained from various depths

TABLE 1
LOCATION OF SOME SELECTED STATIONS WHERE PLANKTON STUDIES WERE MADE
IN ANTARCTIC WATERS, FEBRUARY-MARCH 1965

Station	Geographic area	S. latitude	W. longitude	Depth (m)
250	Marguerite Bay	68°12'	68°24'	540
258	Bellingshausen Sea	68°16'	77°36'	3418
284	"	66°36'	73°56'	3640
351	Bismarck Strait	64°55'	64°15'	306
368	Deception Island	62°58'	60°41'	81
387	Bransfield Strait	61°53'	56°42'	418
403	"	63°15'	58°58'	99
410	Gerlache Strait	63°46'	62°59'	360
414	"	64°54'	62°52'	90

(usually 0, 5, 10, 25, 50, and 100 m) by use of Van Dorn bottles. Qualitative samples of phytoplankton were collected by towing a no. 20 nylon half-meter net diagonally from 50 m to the surface. Quantitative estimates of the plankton species were made by filtering organisms from measured volumes of water onto Millipore filters and then enumerating the species in a Sedgwick-Rafter cell under a compound microscope. Chlorophyll *a* was extracted from Millipore-filtered samples with 90 per cent acetone, then measured photometrically, and the values were calculated by use of the formula proposed by Parsons and Strickland.¹⁰ Carbon assimilation was measured by the carbon-14 technique of Steeman-Nielsen, according to the general procedures outlined by Strickland and Parsons.¹¹ The samples of plankton were incubated for 4 hr in a fluorescent light incubator, cooled by sea water and ice to a temperature approximately equal to the temperature of the local sea water.

The intensity of incident light, and also the light reflected from the surface of the sea, were recorded at numerous stations, using simultaneously upright and inverted Eppley pyrhelimeters and a Bausch and Lomb recorder. Diurnal variations in light were also measured manually every hour with a Weston illumination meter throughout the period of observations during February-March 1965. Penetration of light to different depths in the sea was measured with a G.M. submarine photometer.

Results.—Observations of the phytoplankton in numerous samples of water obtained from standard depths at many stations revealed great variations in the kinds of populations and their physiological activity. The phytoplankton communities studied at stations 258 and 284 in the Bellingshausen Sea were comprised chiefly of *Chaetoceros criophilum* and *Corethron criophilum*, accompanied by *Rhizosolenia alata*, *R. hebetata*, *R. crassa*, *Chaetoceros dictyota*, and some other diatoms. The diatom flora at station 250 in Marguerite Bay contained many small cells of what appears to be *Fragilaria curta*, also *Fragilariopsis antarctica*, *Nitzschia seriata*, *Chaetoceros tortissimum*, *Biddulphia striata*, *Eucampia zodiacus*, *Synedra reinboldi*, *Coscinodiscus* sp., and other less common species. The composition of the plankton of Matha Strait was somewhat similar to that of Marguerite Bay.

The waters at Station 351 in Bismarck Strait and stations 410 and 411 in the Gerlache Strait contained a mixed diatom flora, dominated by *Biddulphia striata*. The Bransfield Strait, at stations 387 and 403, was likewise characterized by the dominance of *Biddulphia striata*, accompanied by *Rhizosolenia alata*, *R. hebetata*, *Chaetoceros tortissimum*, *Nitzschia seriata*, *Corethron criophilum*, *Coscinodiscus* sp., and *Synedra reinboldi*. The waters of Deception Island contained a mixed popula-

tion, consisting of *Thalassiosira hyalina*, various other centric diatoms, and *Dinobryon* sp. in considerable abundance.

Some representative examples of carbon assimilation, determined by incubating different communities of phytoplankton in selected areas, are presented in Figure 1. The phytoplankton of surface waters in Deception Island showed increasing photosynthesis up to a maximum of over 100 mg C/m³/hr at about 2800 ft-c in the incubator. The plankton of the Gerlache Strait region produced about 10 mg C/m³/hr under conditions of light saturation. The waters of Bransfield Strait were somewhat less productive, and the Bellingshausen Sea showed the smallest rate of carbon assimilation, with a maximum of less than 1 mg C/m³/hr in the surface waters.

The penetration of light to various depths, vertical distribution of chlorophyll *a*, and temperatures at different depths are shown for four different regions in Figure 2.

The euphotic zones in Deception Island and the Gerlache Strait were limited to superficial strata somewhat less than 10 m in depth, because of the great abundance of plankton. In contrast, the Bransfield Strait and Bellingshausen Sea, being less densely populated with plankton, were characterized by penetration of light to greater depths, the euphotic zone extending to about 25 and 35 m in these areas.

The temperature of the Bellingshausen Sea was about -1.2°C at the surface, and

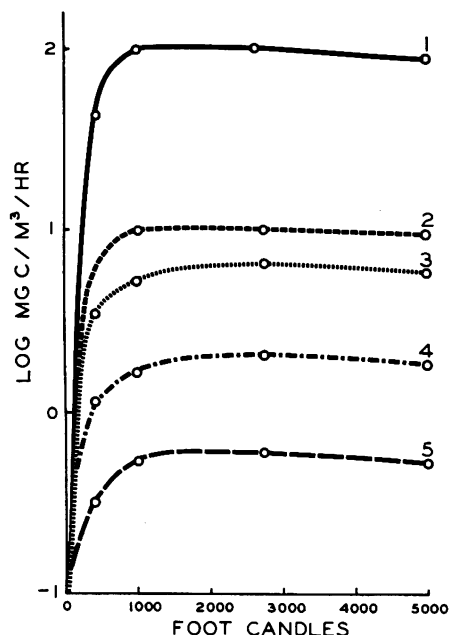


FIG. 1.—Carbon assimilation of some Antarctic phytoplankton collected from surface waters and incubated at different intensities of light. (1) Deception Island; (2) Gerlache Strait; (3, 4) Bransfield Strait; (5) Bellingshausen Sea.

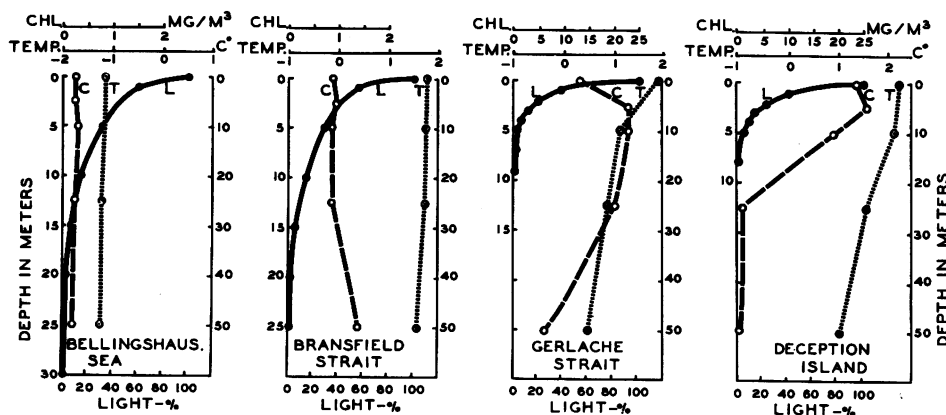


FIG. 2.—Chlorophyll *a* (mg/m³) in curves labeled C, temperature ($^{\circ}\text{C}$) in curves marked T, and relative light values (as % of the light just under the surface) in curves L, for different depths of selected stations in the Bellingshausen Sea, Bransfield Strait, Gerlache Strait, and Deception Island.

nearly isothermic downward throughout the euphotic zone. In Bransfield Strait the temperature of various stations was often about 1.7° at the surface and downward, with slightly colder water near the bottom of the light zone. The Gerlache Strait waters were generally stratified, with warmer water at the surface (2.0°C), and decreasing temperature downward to about 0.5°C at 50 m. In like manner at Deception Island, stratification of the upper layer was indicated by a surface temperature slightly greater than 2.0°C , and decreasing temperature downward to 1.0°C at 50 m. It appears that the Gerlache Strait and Deception Island surface waters are temperature-stratified and somewhat stabilized, whereas some parts of Bransfield Strait and the Bellingshausen Sea remain relatively unstratified in the summer.

An important factor in the planktonic environment in these areas is the available light. Cloudy and overcast days were predominant in the Bellingshausen Sea and Bransfield Strait, with maximum light readings of 3200 ft-c or less on many days. Sunny days were often observed in the Gerlache Strait and Deception Island areas during the Antarctic summer, with typical light maxima of about 6500 ft-c frequently recorded. Integrated light values at Admiral Brown station in the Gerlache Strait during a fairly sunny day on February 4, 1965, gave $650\text{ cal/cm}^2/\text{day}$, in contrast with $172\text{ cal/cm}^2/\text{day}$ during overcast weather in the Bellingshausen Sea on February 11, 1965. Some typical curves for light penetration, measured with a submarine photometer at different depths, are shown in Figure 2. The use of light data in calculations of productivity will be shown at the end of this paper.

The vertical distribution of chlorophyll *a*, as an indication of the amount of plankton in the water columns of the areas under consideration, is shown clearly in the graphs of Figure 2. In the Bellingshausen Sea, chlorophyll *a* values were uniformly low at about 0.2 mg/m^3 throughout the photic zone. At different stations in the Bransfield Strait, chlorophyll *a* occurred in variable amounts from about 0.8 to 5.8 mg/m^3 in the upper 10 m. The great blooms of microalgae occurring in the Gerlache Strait and Deception Island are indicated by very high values of chlorophyll *a*, observed near the surface and extending downward into the hypophotic region below 9 m. Plankton produced near the bottom of the photic zone in the spring may be progressively cut off from light, as the bloom continues to develop into the summer, leaving a portion of the residual crop to exist in darkness at lower levels. Large amounts of diatoms also settle from the photic zone downward into the aphotic region. Divers working during calm weather in midsummer at Melchior Island observed heavy plankton blooms settled onto the floor of the sea, and thick deposits of diatoms covering the macroalgae in shallow waters.

The assimilation numbers determined for phytoplankton collected in seven representative areas, between the South Shetland Islands and Peter the First Island, are presented in the graphs of Figures 3 and 4. The highest maximal values were observed in the range of 2.4–3.0 in near-surface waters of Matha Strait and at stations in the Bellingshausen Sea. In Bismarck Strait and Marguerite Bay the maximal assimilation numbers were 1.0 and 1.2, respectively. In the Gerlache Strait, where the standing crop and surface productivity were relatively great, the $\text{mg C/hr/mg chl } a$ was only about 0.7 in surface waters. In incubation experiments plankton taken from the bottom of the photic zone or from the hypophotic zone often, but not always, showed lower assimilation numbers than did plankton taken from the upper portion of the light region. It is obvious that the dense blooms of

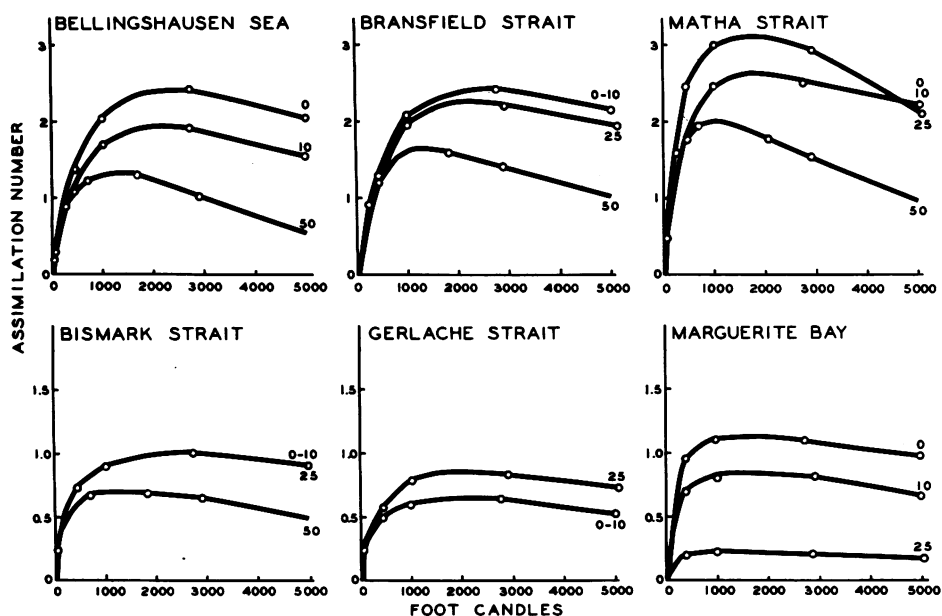


FIG. 3.—Assimilation numbers (mg C/hr/mg chlorophyll *a*) of phytoplankton communities, occurring at different depths in six representative areas, determined for different intensities of light in fluorescent light incubators. The values vary considerably with the light intensity, depth of water, and physiological state of the plankton in different geographic regions.

Biddulphia in the Gerlache Strait are less efficient than the sparsely populated communities of *Corethron* and *Chaetoceros* in the Bellingshausen Sea.

The great abundance of chlorophyll *a* present in the water layer below the photic zone was a striking characteristic of many Antarctic areas studied during February–March 1965. A comparison was made of the relative distribution of chlorophyll *a* in the euphotic zone, i.e., from the surface to a depth where the intensity of light was reduced to 1 per cent of the surface light, and in the hypophotic zone, from a depth where the light was reduced to 1 per cent of its surface value downward to an arbitrarily chosen level, at which the light was only 0.000, 1 per cent of the surface value. When these limits were first chosen for study, the euphotic/hypophotic chlorophyll ratio was found to be 1.0 at Deception Island. This model served as a basis for comparing the relative abundance of pigments present in the zones of other areas (Fig. 5). In the regions where the standing crops were very high, as in the Gerlache Strait and at Deception Island, the total chlorophyll present in the water

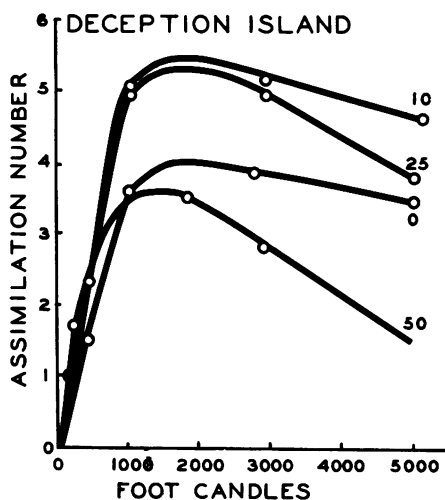


FIG. 4.—Assimilation numbers (mg C/hr/mg chlorophyll *a*) of the plankton collected inside Deception Island were higher than those of all other stations (see Fig. 3).

column, from the surface down to the 0.000, 1 per cent light level, averaged 395 mg/m² for the four representative stations shown in Figure 5. For the four poorer stations located in the Bransfield Strait and Bellingshausen Sea, the corresponding average was only 49 mg/m². The average per cent of the total chlorophyll located in the lower zone was 61 in the rich areas and 66 in the poorer regions. The ratio of assimilation numbers in the euphotic-hypophotic zone in the rich areas was 0.9 and in the poorer regions 1.6.

The behavior of the phytoplankton of Deception Island, a nearly extinct volcanic crater, needs to be considered as a special case. The water column of Foster Bay inside Deception Island shows thermal stratification, and the physical and chemical conditions are different from typical Antarctic waters. The euphotic zone in late February was limited approximately to the upper 8 m (see Fig. 2). The highest value for the assimilation numbers at light saturation in the incubator (Fig. 4) was 5.2 for plankton obtained from 10 to 25 m. The assimilation number at the surface was 3.9, and below the euphotic zone, at a depth of 50 m, the value was 3.5.

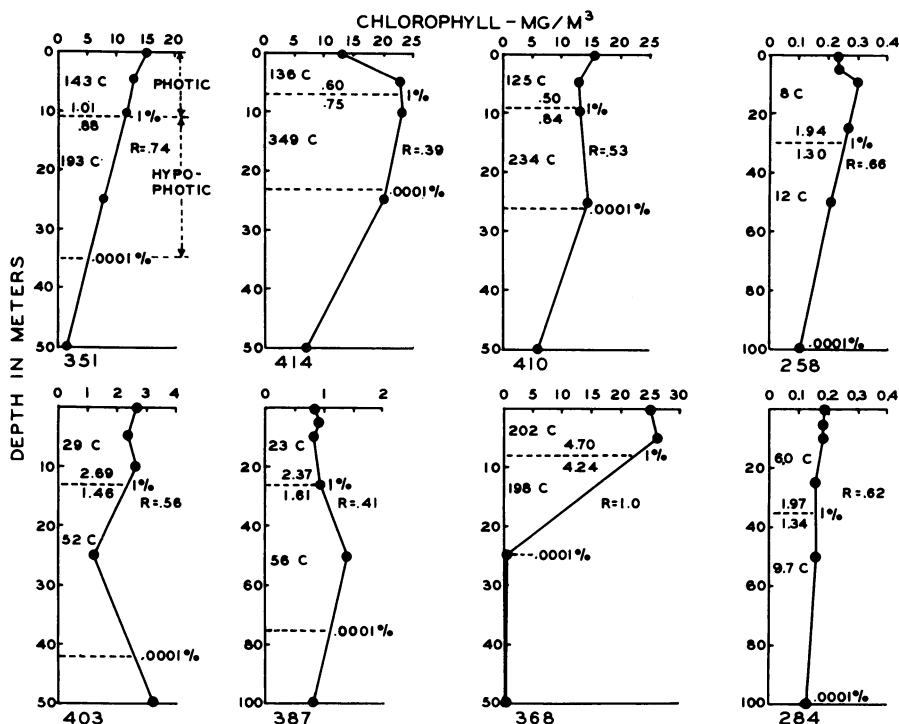


FIG. 5.—Distribution of chlorophyll *a* in the photic zones (from the surface to a depth where the light is reduced to 1% of the surface value) and in the hypophotic layers (in the light range from 1% to 0.000, 1% of the surface value) of eight stations. Numbers 351, 410, and 414 are representative of the Gerlache Strait, 387 and 403 are typical of the Bransfield Strait, 368 is at Deception Island, and 258 and 284 are in the Bellingshausen Sea. The chlorophyll *a* contents of the water columns, calculated for each of the two layers, are shown as mg chl *a*/m² (labeled *C*) in each graph. The ratio of the chlorophyll in the photic and hypophotic zones is indicated by the numbers labeled *R*. Assimilation numbers are shown just above and below the dotted lines which separate the photic and hypophotic layers. Example: at station 351, the euphotic zone extends to about 11 m. The selected hypophotic zone extends below 11 m to about 35 m at this station. The ratio of mg chlorophyll/m² in the photic zone to that in the hypophotic zone, $R = 143/193 = 0.74$. The assimilation number of plankton from the photic zone, when incubated at light saturation, is 1.01; that of the hypophotic zone is 0.88.

The great amount of chlorophyll *a* and the high assimilation numbers, maintained well into the advanced stages of the bloom period, result in rapid rates of organic production at Deception Island.

Several conclusions can be drawn from the observations which we have made, although explanations for all of the data cannot easily be derived from the known facts. The standing crops in isothermal waters are very much less than in waters which show stratification. The euphotic zone varies from about 8 m in stratified water masses to approximately 35 m in isothermal water columns of oceanic areas. The assimilation numbers are lowest in areas having high chlorophyll *a* content and larger standing crops of the diatom *Biddulphia striata*. Highest assimilation numbers are associated with the abundant *Thalassiosira hyalina*, occurring in Deception Island. More than half of the chlorophyll *a* in the abundant standing crops of Antarctic phytoplankton was calculated to be present below the euphotic zone, in both isothermal and stratified waters. It seems probable that relatively low efficiency of photosynthesis in the older blooms observed in the Gerlache Strait during late February 1965 may be related to metabolic deterioration of senescent populations. Perhaps studies made earlier in the spring season would reveal higher

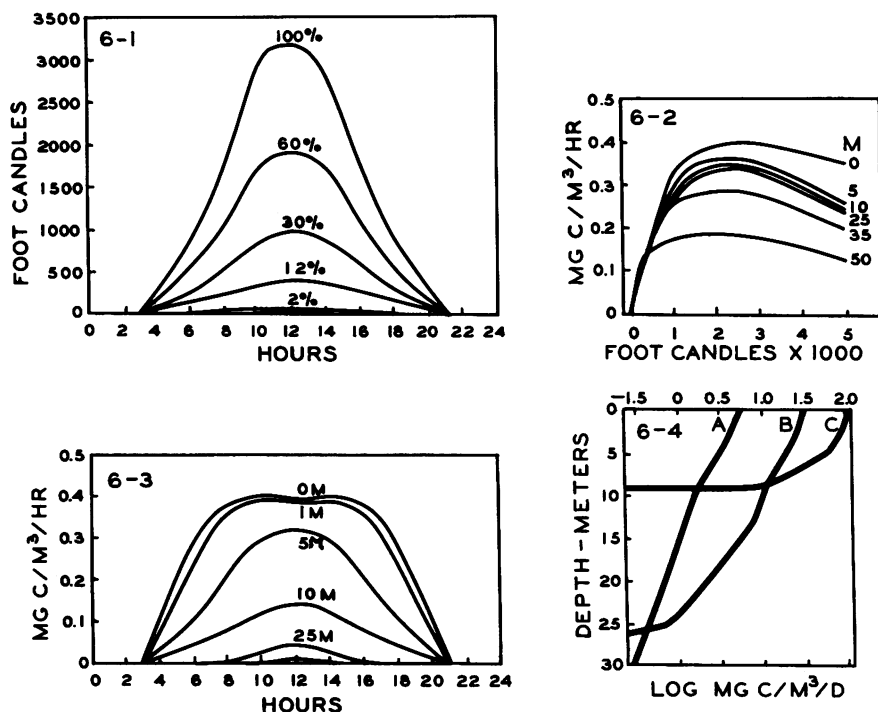


FIG. 6.—An example of graphic calculations of primary production of a water column in the Bellingshausen Sea to yield a productivity value, expressed as $\text{mg C/m}^2/\text{day}$. In 6-1, diurnal light curves corresponding to various depths from the surface to 30 m with light penetration of 100, 60, 30, 12, 2, and 1% of the surface values, and in 6-2 the photosynthesis light curves of plankton obtained from different depths down to 50 m are shown. Calculations of carbon fixation for the diurnal light intensities at different depths are shown in 6-3. In 6-4A, a plot of the logarithm of daily carbon fixation ($\text{mg C/m}^2/\text{day}$) at each depth to the bottom of the euphotic zone (1% light) gives a curve whose under area can be integrated to yield $\text{mg C/m}^2/\text{day}$. Values for daily productivity of plankton in the Bransfield and Gerlache Straits are also shown in 6-4B and C, respectively.

assimilation numbers in physiologically younger *Biddulphia* blooms. It is clear that the assimilation numbers for different communities of Antarctic surface phytoplankton vary greatly in the present experiments over the range of about 0.5–5.2, depending upon the species composition of the communities, the natural history of the organisms, and their adaptations to environmental conditions. Even higher values (about 8.0) have been observed on other cruises in the South Shetland region.¹²

Although it is not the purpose of this paper to report detailed data on primary productivity, it seems desirable to illustrate the use which can be made of physiological data for calculating organic production of water columns in Antarctica. An example of the method is given in Figure 6, with data for a station in the Bellingshausen Sea. The integrated values, in mg C/m²/day, obtained for the water columns of three exemplary stations are as follows: Bellingshausen Sea, 40; Bransfield Strait, 273; and Gerlache Strait, 646. It appears that both physiological condition and species composition of the plankton are important in making calculations of productivity based upon chlorophyll and light data (see ref. 13). A fuller account of the organic productivity in this area of Antarctica will be presented in another contribution.¹⁴

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